

THE AMERICAN NATURALIST

VOL. XLIX.

September, 1915

No. 585

A STUDY OF ASYMMETRY, AS DEVELOPED IN THE GENERA AND FAMILIES OF RECENT CRINOIDS

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PREFACE

IN the animal kingdom there are few, if any, forms which can be properly described as perfectly symmetrical, either from a bilateral or a radial standard. We have, however, become accustomed to refer to many types as "asymmetrical." In the sense in which we employ this word we do not intend to convey the meaning that these types alone of their respective classes depart from true bilateral or radial symmetry, but rather to indicate that they exhibit more asymmetry than the maximum contemplated in our generalized concept of, or arbitrary standard for, those classes.

Thus we readily recognize and confess the asymmetry in the skull of the narwhal (*Monodon*) with its single greatly elongated and twisted incisor, and the asymmetry in the bones in the skull of the whales, while at the same time we commonly consider man to be symmetrical, though careful measurement shows the right arm and

hand to be larger than the left, and the left leg and foot to be larger than the right.

It is clear, therefore, that in dealing with asymmetry in any group we must work inward from the most asymmetrical types toward the least asymmetrical, arbitrarily erecting a barrier between what we call asymmetry and what we are pleased to consider as "symmetry" at any point we choose.

Asymmetry—that is to say the maximum departure from perfect bilateral or radial symmetry—appears to follow certain definite lines wherever it appears, quite regardless of the type of animal, or the form, in which it is manifested.

In the following pages we shall consider the wider variations from the typical pentamerous symmetry among the recent erinoids, which is phylogenetically most extensively developed at the consummation of the phylogenetic lines, and physico-economically most extensively developed in the situations most unsuited to erinoidal existence, particularly in the very warm water of the East Indian and north Australian littoral, and the very cold water of the Antarctic regions and the deep abysses of the oceans, and is least evident among phylogenetically conservative types, and in the situations which appear to be best suited for erinoid life.

As an indication of the possible fundamental importance of the light thrown on the study of asymmetry by an examination of the data offered by the recent erinoids, it may be noticed and borne in mind that among the mammals the phylogenetically aberrant asymmetrical narwhal (*Monodon*) is exclusively arctic; the phylogenetically aberrant asymmetrical whales occupy a habitat very aberrant for the class; and the anthropoid apes, which are pronouncedly right or left handed, live in very warm regions; that among the birds the curious crook-billed plover (*Anarhynchus*), with the beak twisted to the right and one side of the body lighter in color than the other, occurs only in New Zealand, the home of many phyloge-

netic oddities; the hornbill *Rhinoplax*, with an asymmetrical tail, further peculiar in having a solid casque, an elongate central rectrix, and a naked patch on the back extending to the sides of the head, is found in the warm Malayan region; the crossbills (*Loxia*), with the tips of the mandibles crossed and a corresponding distortion in the bones of the head are all subarctic or cold temperate forms; and the owls with one ear greatly larger than the other, so far as has been determined are, like the crossbills, birds of the colder regions; and that among the fishes and similar types the very asymmetrical *Anableps* lives in the warm tropical littoral, while the flatfishes (Pleuronectidæ) are chiefly developed in the warm tropical littoral, and in cold and shallow water, and the asymmetrical forms of "Amphioxus" (using the term in its broadest sense) occur in warm and shallow water.

Further it is interesting to recall that animals under domestication—that is, living under conditions which typically lead to a more or less degenerate diversity in form and color—commonly develop asymmetry of action which, though usually occurring in the form of individual variation, may become very marked as in the case of the Japanese waltzing mice, as well as pronounced, though irregular and sporadic, asymmetry in color pattern, dentition, and other features.

More or less pronounced asymmetry undoubtedly exists in many types in which up to now it has been overlooked, and the conclusions reached in the present paper may be modified somewhat when a better knowledge of the subject is attained; but on the other hand it is scarcely probable that many instances of marked asymmetry have escaped the notice of naturalists.

THE DIFFERENT TYPES OF CRINOIDAL ASYMMETRY

In the great majority of the recent crinoids the body is almost perfectly pentamerous, being composed of five similar sectors. The presence of a small muscular cone in the posterior interradius, at the summit of which is

the posterior opening of the spiral digestive tube, gives the only visible indication of a departure from true pentamerous symmetry.

In certain types, however, a more or less marked deviation from the characteristic symmetry occurs. This deviation follows four different lines:

1. A rearrangement of the five primary groove trunks upon the disk whereby (*a*) the left posterior increases in size and gives off more branches than any of the others; (*b*) as a result of the anterior migration of the mouth, the two posterior become much longer and the anterior much shorter than the others and a condition of bilateral symmetry is attained; (*c*) correlated with the anterior migration of the mouth, all of the primary groove trunks become merged into a horse-shoe shaped ring which skirts the lateral and anterior borders of the disk, giving off branches to the arms, the mouth being in the right center of the ring so that the ambulacra on the left are more developed than those on the right, or the ambulacra leading to the left posterior arm disappearing altogether so that the ambulacra on the right are more developed than those on the left;

2. A dwarfing, or an overdevelopment, of the left posterior, more rarely of both, posterior radials with their post-radial series;

3. The intercalation of additional radials and post-radial series which alternate with the original five, and the associated dropping out of one of the five radials; and

4. The suppression of two of the primarily five basals.

THE ASYMMETRICAL CRINOIDS

In the following list are given all the families and genera of recent crinoids which include asymmetrical species.

After the families the bathymetrical and thermal ranges are given, and after the genera the bathymetrical range.

Certain families are represented in the warm littoral

water of the Malayan region and northern Australia, but the highest actual temperature record is considerably less than the temperature of this water; in these cases the temperature 80.5° is given after the ascertained maximum as more nearly representing the true maximum.

Of the nine families the four in which asymmetry is most markedly developed are marked with an asterisk (*); and of the twenty-seven genera the sixteen which include the most notably asymmetrical species are similarly distinguished.

	Depth (Fathoms)	Temperature (F.)
Capillasterinæ	0-830	44.5-78.5 (80.5)
<i>Comatella</i>	0-106	
<i>Neocomatella</i>	10-830	
<i>Palrocomatella</i>	140-153	
<i>Capillaster</i>	0-160	
<i>Nemaster</i>	0-194	
<i>Comissia</i>	0-100	
<i>Leptonemaster</i>	42-163	
Comactiniinæ	0-288	62.0-71.9 (80.5)
* <i>Comatula</i>	0-160	
<i>Comatulella</i>	0-10	
<i>Cominia</i>	0-288	
<i>Comactinia</i>	0-262	
*Comasterinæ	0-140	52.3-80.0 (80.5)
* <i>Comaster</i>	0-95	
* <i>Comantheria</i>	0-83	
* <i>Comanthina</i>	0-42	
* <i>Cemanthus</i>	0-140	
Heliometrinæ	2-1,600	28.7-60.5
* <i>Promachocrinus</i>	10-222	28.7
Pentametrocrinidæ	103-1,800	33.5-60.6
* <i>Thaumatoocrinus</i>	361-1,800	
*Apiocrinidæ	565-940	36.7-38.1
* <i>Proisocrinus</i>	940	
* <i>Carpenterocrinus</i>	565	
Bourguetierinidæ	62-2,690	29.1-70.7
* <i>Rhizocrinus</i>	77-1,300	32.2-48.7
<i>Monachoocrinus</i>	687-2,419	37.4-40.0
*Holopodidæ	5-120	71.0
* <i>Holopus</i>	5-120	
*Plicatoocrinidæ	266-2,575	31.1-43.9
* <i>Calamoocrinus</i>	392-782	
* <i>Ptilocrinus</i>	266-2,485	
* <i>Hyocrinus</i>	1,600-2,575	
* <i>Gephyrocrinus</i>	992-1,103	
* <i>Thalasseocrinus</i>	1,262-2,325	

THE PHYLOGENETIC DISTRIBUTION OF ASYMMETRY

The phylogenetic distribution of the asymmetry among the recent crinoids is very interesting.

Asymmetry is almost universal in the comatulid family Comasteridæ, which includes the most specialized of all recent forms; in this family the first and second types occur, though the latter is much less common.

Asymmetry is characteristic of the genus *Promachocrinus*, which is probably rightly considered as the most specialized genus in the subfamily Heliometrinæ, the largest and most universally distributed subfamily of the at present dominant family Antedonidæ; in the genus *Promachocrinus* the first and third types occur.

Asymmetry is equally characteristic of the genus *Thaumatoocrinus*, the most specialized genus of the family Pentametrocrinidæ; in this genus the third type is found.

Asymmetry exists in all of the genera of the Plicocrinidæ, which includes the last highly specialized exponents of the ancient order Inadunata, which flourished from the Ordovician to the Carboniferous, with one family extending into the Permian and Trias and another (the present family) appearing in the Jura; in the Plicocrinidæ the first, second and fourth types occur in recent genera, while the third is also found in fossil genera.

Asymmetry is characteristic of both of the recent genera of Apiocrinidæ, which are the most specialized genera in the family; in these the second type occurs.

Asymmetry of the second type is characteristic of the only recent genus of the Holopodidæ.

Asymmetry characterizes both of the species of *Rhizocrinus*—which is at least as highly specialized as any of the genera of the Bourguetierinidæ—existing in the present seas, and one of the species of *Monachocrinus*, a genus of which the exact phylogenetic position is uncertain, although it is probably on a par with *Rhizocrinus*; in these the third type occurs.

In the following list the recent asymmetrical types are

given in the order of the extent of their departure from the normal pentamerous symmetry:

Plicatoerinidæ:	Asymmetry of Types 1, 2, (3) and 4.
Comasteridæ:	Asymmetry of Types 1 and 2.
<i>Promachocrinus</i> :	Asymmetry of Types 1 and 3.
Apioerinidæ:	Asymmetry of Type 2.
Holopodidæ:	Asymmetry of Type 2.
<i>Thaumatocrinus</i> :	Asymmetry of Type 3.
<i>Rhizocrinus</i> :	Asymmetry of Type 3.
<i>Monachocrinus</i> :	Asymmetry of Type 3.

The asymmetry of the Comasteridæ is considered more fundamental than that of *Promachocrinus* for the reason that it is characteristic of practically the entire family, and also because it results in a much greater degree of irregularity. It is interesting to note that asymmetry of Type 3 is not uncommon among the Comasteridæ, in the form of individual variation.

The asymmetry of the Apioerinidæ and Holopodidæ is considered more fundamental than that of the genus *Thaumatocrinus* for the reason that it affects the entire family, at the same time inducing a greater departure from the normal form.

The asymmetry of *Rhizocrinus* is considered less fundamental than that of *Thaumatocrinus* because, though affecting all of the species, exactly as in *Thaumatocrinus*, it is less extensively developed.

The asymmetry of *Monachocrinus* affects only one of the seven species of the genus.

Briefly stated, it appears that, no matter in what form it may manifest itself, metameric asymmetry in the recent crinoids is an attribute of the most specialized types in the groups in which it occurs.

From the conditions in the Plicatoerinidæ, the last remnants of the once abundant Inadunata, it would appear that asymmetry is an attribute of phylogenetically decadent types—types in which type senescence has so far advanced as to inhibit the normal course of development.

THE GEOGRAPHICAL DISTRIBUTION OF ASYMMETRY

The geographical distribution of asymmetry is as interesting as the phylogenetical distribution.

Although occurring everywhere except in the Arctic Ocean and in the Mediterranean, Bering, Okhotsk and Japan seas, asymmetrical types are most frequent and most highly developed (1) in warm shallow water from southern Japan southward throughout the Malay Archipelago to northern Australia and westward to Ceylon, and (2) in the Antarctic and in the cold abysses.

Though present among species inhabiting the west Atlantic from North Carolina to Brazil, and characteristic of many forms living at intermediate depths in the western Pacific and in the Indian Oceans, in these it is never more than slightly developed, even though they be very closely related to types in which it is, in other situations, carried to an extreme.

Depth (Fathoms)	Number of Asymmetrical Genera	Number of Symmetrical Genera	Per Cent. of the Latter Represented by the Former
0-50	16	50	32%
50-100	15	53	28
100-150	13	51	25
150-200	10	44	22
200-250	5	39	13
250-300	5	34	14
300-350	3	30	10
350-400	4	32	12
400-450	5	29	17
450-500	5	27	18
500-550	5	26	19
550-600	6	26	23
600-650	5	26	19
650-700	6	22	27
700-750	6	22	27
750-800	6	18	33
800-850	5	18	28
850-900	4	18	22
900-950	5	19	26
950-1,000	5	16	31
1,000-1,100	5	16	31
1,100-1,200	5	12	41
1,200-1,300	5	9	55
1,300-1,400	4	9	44
1,400-1,500	4	7	57
1,500-1,600	4	7	57
1,600-1,700	5	3	166
1,700-1,800	5	3	166
1,800-1,900	4	3	133
1,900-2,000	4	3	133
2,000-2,500	4	3	133
2,500-3,000	1	3	33

In short, though almost universal, occurring every-



FIG. 1. The Relation between the Genera with and without Asymmetrical Species at Different Depths (—), with very Asymmetrical and without Asymmetrical Species at Different Depths (- - -), and the Decrease in the Number of Genera with Depth, expressed in Percentages of the Total Number (· · ·).

where except in inland seas, asymmetry is especially developed in the warm waters of the eastern tropics, particularly in the Malayan region and in northern Australia, and in the Antarctic and the cold abysses.

BATHYMETRICAL DISTRIBUTION OF THE ASYMMETRICAL CRINOIDS

The number of genera of recent crinoids including asymmetrical species, the number of genera including

Depth (Fathoms)	Number of Asymmetrical Genera Which Are Marked *	Number of Symmetrical Genera	Per Cent. of the Latter Represented by the Former
0-50	7	50	14.0
50-100	7	53	13.2
100-150	5	51	9.8
150-200	3	44	6.8
200-250	2	39	5.1
250-300	2	34	5.8
300-350	2	30	6.6
350-400	4	32	12.5
400-450	4	29	13.8
450-500	4	27	14.8
500-550	4	26	15.4
550-600	5	26	19.2
600-650	4	26	15.4
650-700	4	22	18.1
700-750	4	22	18.1
750-800	4	18	22.2
800-850	3	18	16.6
850-900	3	18	16.6
900-950	4	19	21.0
950-1,000	4	16	25.0
1,000-1,100	4	16	25.0
1,100-1,200	4	12	33.3
1,200-1,300	4	9	44.4
1,300-1,400	3	9	33.3
1,400-1,500	3	7	42.8
1,500-1,600	3	7	42.8
1,600-1,700	4	3	133.3
1,700-1,800	4	3	133.3
1,800-1,900	3	3	100.0
1,900-2,000	4	3	100.0
2,000-2,500	3	3	100.0
2,500-3,000	1	3	33.3

only symmetrical species, and the percentage of the number of symmetrical genera represented by the number of asymmetrical genera at different depths are given in the table on page 528 and shown in Fig. 1.

Considering the percentages only, these may be regrouped as follows:

0- 200	27
200- 650	16
650-1,100	28
1,100-3,000	92

Considering only the genera marked with an asterisk (*) we find the representation at different depths given in the table on page 530 and in Fig. 1.

Considering the percentages only, these may be re-grouped, as follows:

0- 100	13.6
100- 350	6.8
350- 900	16.6
900-3,000	61.8

The number of families of recent crinoids including asymmetrical species, the number of families including only symmetrical species, and the percentage of the number of families including only symmetrical species represented by the number of families including asymmetrical species at different depths, are shown in the table on page 533 and in Fig. 2.

The proportion of the genera including asymmetrical species to those composed entirely of symmetrical species, about one third between the shore line and 50 fathoms, decreases to a minimum of one tenth at from 300 to 350 fathoms, and then increases, with greater and greater rapidity, to 1,600 fathoms and below.

It is everywhere less than one quarter between 100 and 650 fathoms. Thus it is evident that the genera including asymmetrical species are chiefly developed in shallow water, and in deep water, and are least developed in water of intermediate depth.

Taking the ocean as a whole, the temperature at 100 fathoms is 60.7°, and at 650 fathoms 38.6°; the optimum temperature for the recent crinoids appears to be between 50° and 65°; when we remember that most of the asymmetrical species, and all of the most asymmetrical ones, in the genera which give us our numbers for 0-50 and for 50-100 fathoms, are confined to a littoral belt of scarcely more than 50 fathoms, it becomes at once evident that asymmetry among the crinoids is developed chiefly in

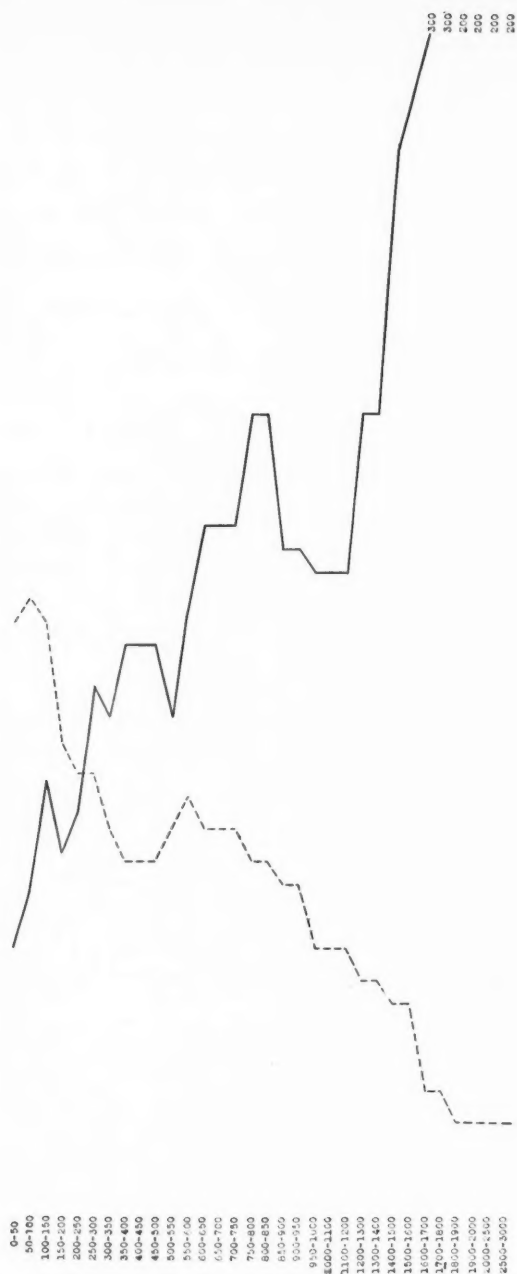


FIG. 2. The Proportion of Families with and without Asymmetrical Species at Different Depths (—), and the Percentage of the Total Number of Crinoid Families represented at Different Depths (---).

Depth (Fathoms)	Number of Asymmetrical Families	The Families Marked with an *	Number of Symmetrical Families	Per Cent. of Sym- metrical Families Represented by the Asymmet- rical
0-50	5	2	15	33
50-100	6	2	15	40
100-150	7	2	13	54
150-200	5	0	11	45
200-250	5	0	10	50
250-300	6	0	9	66
300-350	5	0	8	62
350-400	5	0	7	71
400-450	5	0	7	71
450-500	5	0	7	71
500-550	5	0	8	62
550-600	6	1	8	75
600-650	6	1	7	86
650-700	6	1	7	86
700-750	6	1	7	86
750-800	6	1	6	100
800-850	6	1	6	100
850-900	5	1	6	83
900-950	5	1	6	83
950-1,000	4	0	5	80
1,000-1,100	4	0	5	80
1,100-1,200	4	0	5	80
1,200-1,300	4	0	4	100
1,300-1,400	4	0	4	100
1,400-1,500	4	0	3	133
1,500-1,600	4	0	3	133
1,600-1,700	3	0	1	300
1,700-1,800	3	0	1	300
1,800-1,900	2	0	1	200
1,900-2,000	2	0	1	200
1,900-2,000	2	0	1	200
2,000-2,500	2	0	1	200
2,500-3,000	2	0	1	200

water above and below the optimum, and least at and just below the optimum temperature.

Considering only the genera marked with an asterisk (*), that is, the genera with the most highly developed asymmetry, we find the same general facts emphasized as in the case of all the genera including asymmetrical forms; but here the minimum is between 50 and 400 fathoms instead of between 100 and 650 fathoms. The temperature at 400 fathoms is 41.8° . This approximation of the minimum to the zone of optimum temperature when only the most asymmetrical types are considered strengthens the hypothesis that the zone of optimum temperature really represents the zone of least-developed asymmetry.

Comparing the proportionate abundance of asymmetrical genera at different depths with the frequency of all the genera expressed as percentages of the total, we find that the former decreases while the latter increases to 50-100 fathoms; from this point the two run roughly parallel to 300-350 fathoms, after which the former increases with progressively greater rapidity, while the latter decreases steadily and gradually to 3,000 fathoms; the two cross each other between 600 and 700 fathoms.

The proportion of the families including asymmetrical species to those composed entirely of symmetrical species increases from one third at 0-50 fathoms to three times as many at 1,600 fathoms and twice as many at 1,900 fathoms and over. The increase, though irregular—largely as a result of the small numbers involved at the greater depths—is constant.

The number of families at different depths, expressed as percentages of the total number, increases from 0-50 to 50-100 fathoms, and then decreases to 1,800 fathoms and beyond. Except for a minimum between 350 and 500 fathoms the decrease is fairly regular.

The two lines cross between 200 and 300 fathoms.

The reversal of the direction of the line representing the frequency of the families including asymmetrical species as a percentage of the number of the families not including asymmetrical species at different depths, as compared with the line representing the frequency of the families at different depths expressed as percentages of the total number, indicates that the less favorable the environment for crinoids as a whole the greater becomes the proportion of asymmetrical forms.

In the proportion of genera including asymmetrical species to those composed entirely of symmetrical species we find a minimum between 100 and 650 fathoms or, considering only the most markedly asymmetrical types, between 50 and 400 fathoms, the numbers above 100 (or 50) fathoms and below 650 (or 400) fathoms being greater.

Considering families in the same light we appear to

have an increase between 350 and 500 fathoms—that is, more or less coinciding with this minimum.

In the frequency of families at different depths expressed as percentages of the total number we notice a minimum between 350 and 500 fathoms which reaches a point not again touched until 750–800 fathoms and beyond.

This indicates the occurrence here of a proportionately large number of families including asymmetrical species, but at the same time a proportionately small number of genera including asymmetrical species within those families.

THERMAL DISTRIBUTION OF THE ASYMMETRICAL CRINOIDS

In examining the thermal distribution of asymmetry among the recent crinoids we find it advisable to employ family instead of generic units, for the reason that our records are insufficient to furnish us with even approximate thermal ranges for many of the individual genera, though in most cases these may be estimated with reasonable exactness. The records for the crinoids of the deeper water are far more satisfactory than the records for the crinoids of the littoral, and this is very fortunate, for it justifies us in assigning a temperature of 65° and over to a number of species and genera which are of great importance in the present study.

In considering asymmetry in relation to temperature by family units it must constantly be borne in mind that, whereas certain families (Capillasterinæ, Comactiniinæ and Comasterinæ) extend from the warm littoral into moderately deep water with a relatively low temperature, the asymmetry among their component genera and species is strongly marked only in very shallow water of high temperature, and is only slightly marked—indeed not infrequently entirely absent, as in *Comatilia*—in genera and species inhabiting deep and cold water.

Thus through a study of family units the amount of asymmetry shown at intermediate temperatures is really exaggerated, and appears in its relation to the higher

and to the lower temperatures considerably greater than it really is.

In the subfamily Heliometrinæ, the largest and most widely distributed subfamily of the Antedonidæ, which itself is the dominant crinoid family of the present seas, the range of temperature is very great; but as only one out of the ten genera of the Heliometrinæ is asymmetrical it has seemed sufficient to consider and to tabulate the temperature of this genus (*Promachocrinus*) alone.

The frequency of the families including asymmetrical crinoids at different temperatures is as follows:

85-80°	4
80-75	4
75-70	4
70-65	3
<hr/>	
65-60	4
60-55	3
55-50	3
<hr/>	
50-45	3
45-40	4
40-35	5
35-30	4
30-25	1

These frequencies fall into the following groups:

Below 30°	1
30-45	4.3
45-65	3.2
65-85	3.7

or,

Below 30°	1
30-45	4.3
45-70	3.2
70-85	4.0

Considering the zone of optimum temperature (50°-65°) in contrast to the temperatures above and below, and omitting the exceptionally low temperatures below 30°, we have:

30-55°	3.8
50-65	3.3
65-80	4.0

Bearing in mind always that the frequency between the warm littoral and the cold abyssal temperatures is exaggerated because of the segregation in the warm littoral zone of the most asymmetrical genera and species in many of the families inhabiting intermediate temperatures, it is clear that asymmetry is least developed at the optimum temperature for crinoid life, and most developed in temperatures which are phylogenetically too warm or too cold.

This agrees perfectly with what we found from an examination of the bathymetrical distribution of asymmetry.

A comparison between the frequency of the families of crinoids represented in the recent seas, including only symmetrical species, given in the actual numbers and also as percentages of the total numbers, and the frequency of the families including asymmetrical species, given in the same way, follows (Fig. 3):

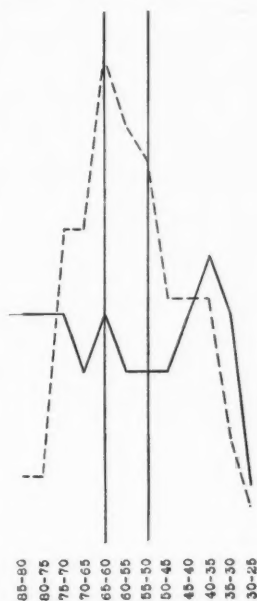


FIG. 3. Frequency at Different Temperatures of the Families Including Asymmetrical Species (—), and those including Symmetrical Species only (---).

Temperature (Fahrenheit)	Families with Symmetrical Species Only	Per Cent. of Total	Families with Asymmetrical Species	Per Cent. of Total
85°-80°	2	13	4	44
80-75	2	13	4	44
75-70	9	60	4	44
70-65	9	60	3	33
65-60	14	93	4	44
60-55	12	80	3	33
55-50	11	73	3	33
50-45	7	47	3	33
45-40	7	47	4	44
40-35	7	47	5	55
35-30	3	20	4	44
30-25	1	7	1	11

THE ASYMMETRICAL FEATURES IN DETAIL

In the following list are given the four types of asymmetry occurring in the recent crinoids, with their geographical distribution and the genera in which they are found.

1. *Disk Not Radially Symmetrical*

Geographical Distribution.—Southern Japan southward to Samoa, Fiji and southern Australia, thence west-

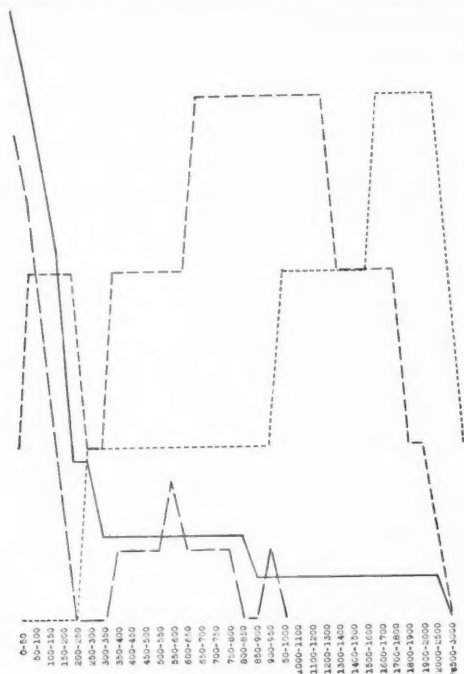


FIG. 4. Frequency at Different Depths of the Genera with Asymmetrical Disks (—), the Genera with One or More Rays Dwarfed or Enlarged (— — —), the Genera with Six to Ten Rays (- - - -), and the Genera with Three Basals (- . . . -), expressed as Percentages of the Total Number in Each Class.

ward to east Africa, from the Red Sea to the Cape; north-western Africa and southwestern Europe (in moderately deep water), and from South Carolina to Brazil; antarctic regions, littoral to abyssal, and northward along the

eastern shores of the Pacific (in deep water) to British Columbia.

This character is most strongly marked in the shallow water from the Marshall Islands and New Caledonia through the Malay Archipelago and along the northern coasts of Australia, and thence westward to Ceylon; and again in the antarctic regions and the abysses of the east Pacific.

Systematic Distribution.—

	Capillasterinæ
<i>Comatella</i>	<i>Capillaster</i>
<i>Neocomatella</i>	<i>Nemaster</i>
<i>Palæccomatella</i>	<i>Comissia</i>
	<i>Leptonemaster</i>
	Comactiniinæ
<i>Comatula</i>	<i>Cominia</i>
<i>Comatulella</i>	<i>Comactinia</i>
	Comasterinæ
<i>Comaster</i>	<i>Comanthina</i>
<i>Comantheria</i>	<i>Comanthus</i>
	Helioetrinæ
	<i>Promachocrinus</i>
	Plicatoerinidæ
	<i>Ptilocrinus</i>

2. *One or More Rays Dwarfed, or Enlarged*

Geographical Distribution.—

Malayan region and north Australia, and Caribbean Sea, but only in warm and shallow water; Malay Archipelago to southern Japan, and Galápagos Islands to Central America in deep cold water.

Systematic Distribution.—

	Capillasterinæ
	<i>Capillaster</i> (part)
	Comactiniinæ
	<i>Comatula</i>
	Comasterinæ
<i>Comaster</i> (part)	<i>Comanthina</i>

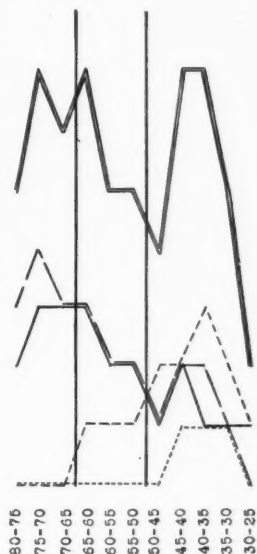


FIG. 5. Frequency at Different Temperatures of Families Including Species in which the Disk is not Radially Symmetrical (—), Families Including Species with one or More Rays Dwarfed or Enlarged (— — —), Families Including Species with from Six to Ten Rays (----), and Families Including Species with Three Basals (-----), and the Total of all these Irregularities.

Comantheria (part)*Comanthus* (part)

Apiocerinidæ

*Proisocrinus**Carpenterocrinus*

Holopodidæ

Holopus

Plicatoerinidæ

Calamocrinus

3. Six to Ten (Sometimes Four) Rays

Geographical Distribution.—Southern Japan and the Hawaiian Islands to the Malay Archipelago, in rather deep water; abysses of the Indian Ocean and the Antarctic; Florida northward and northeastward to Iceland and Norway in deep and cold water.

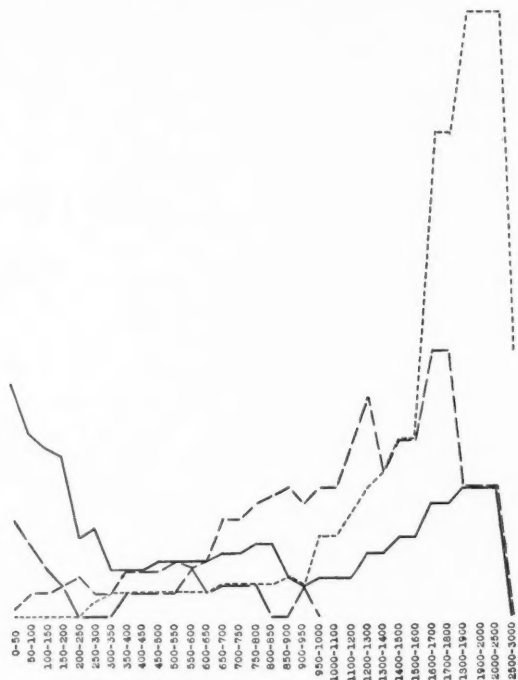


FIG. 6. Proportion at Different Depths of Genera only Symmetrical Species, and Genera including Species with Asymmetrical Disks (—), Genera including Species with One or More of the Rays Dwarfed or Enlarged (— — —), Genera including Species with from Six to Ten Rays (— · — · —), and Genera including Species with Three Basals (· · · · ·).

This feature as an individual variant occurs in the warm water of the Malayan region, in the shallower portions of the Caribbean Sea, and very commonly on the tropical Brazilian coast.

Depth (Fathoms)	Disk Not Radially Sym- metrical (17)	One or More Rays Dwarfed or Enlarged (10)	Six to Ten Rays (4)	Three Basals (4)	Total (35)
0-50	(15) 88	(7) 70	(1) 25	0	(23) 66
50-100	(13) 76	(6) 60	(2) 50	0	(21) 60
100-150	(11) 65	(4) 40	(2) 50	0	(17) 49
150-200	(9) 53	(2) 20	(2) 50	0	(13) 37
200-250	(4) 23	0	(2) 50	0	(6) 17
250-300	(4) 23	0	(1) 25	(1) 25	(6) 17
300-350	(2) 12	0	(1) 25	(1) 25	(4) 11
350-400	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
400-450	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
450-500	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
500-550	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
550-600	(2) 12	(2) 20	(2) 50	(1) 25	(7) 20
600-650	(2) 12	(1) 10	(2) 50	(1) 25	(6) 17
650-700	(2) 12	(1) 10	(3) 75	(1) 25	(7) 20
700-750	(2) 12	(1) 10	(3) 75	(1) 25	(7) 20
750-800	(2) 12	(1) 10	(3) 75	(1) 25	(7) 20
800-850	(2) 12	0	(3) 75	(1) 25	(6) 17
850-900	(1) 6	0	(3) 75	(1) 25	(5) 14
900-950	(1) 6	(1) 10	(3) 75	(1) 25	(6) 17
950-1,000	(1) 6	0	(3) 75	(2) 50	(6) 17
1,000-1,100	(1) 6	0	(3) 75	(2) 50	(6) 17
1,100-1,200	(1) 6	0	(3) 75	(2) 50	(6) 17
1,200-1,300	(1) 6	0	(3) 75	(2) 50	(6) 17
1,300-1,400	(1) 6	0	(2) 50	(2) 50	(5) 14
1,400-1,500	(1) 6	0	(2) 50	(2) 50	(5) 14
1,500-1,600	(1) 6	0	(2) 50	(2) 50	(5) 14
1,600-1,700	(1) 6	0	(2) 50	(3) 75	(6) 17
1,700-1,800	(1) 6	0	(2) 50	(3) 75	(6) 17
1,800-1,900	(1) 6	0	(1) 25	(3) 75	(5) 14
1,900-2,000	(1) 6	0	(1) 25	(3) 75	(5) 14
2,000-2,500	(1) 6	0	(1) 25	(3) 75	(5) 14
2,500-3,000	0	0	0	(1) 25	(1) 3

Temperature (Fahrenheit)	Disk Not Radially Sym- metrical	One or More Rays Dwarfed or Enlarged	Six to Ten Rays	Three Basals	Total
80°-75°	2	3	0	0	5
75-70	3	4	0	0	7
70-65	3	3	0	0	6
65-60	3	3	1	0	7
60-55	2	2	1	0	5
55-50	2	2	1	0	5
50-45	1	1	2	0	4
45-40	2	2	2	1	7
40-35	1	2	3	1	7
35-30	1	1	2	1	5
30-25	1	0	1	0	2

Systematic Distribution.—

Heliometrinæ
Promachocrinus
Pentametrocrinidæ
Thaumatoocrinus
Bourguetierinidæ

Monachocrinus (part)*Rhizocrinus*

Depth (Fathoms)	Number of Genera with Asymmetrical Disks	Number of Genera with Symmetrical Disks	The Number of Genera having Asymmetrical Disks Expressed as a Percentage of the Number with Symmet- rical Disks
0-50	15	51	29
50-100	13	55	23
100-150	11	53	21
150-200	9	45	20
200-250	4	40	10
250-300	4	35	11
300-350	2	31	6
350-400	2	34	6
400-450	2	32	6
450-500	2	30	7
500-550	2	29	7
550-600	2	30	7
600-650	2	29	7
650-700	2	26	8
700-750	2	26	8
750-800	2	22	9
800-850	2	21	9
850-900	1	21	5
900-950	1	23	4
950-1,000	1	20	5
1,000-1,100	1	20	5
1,100-1,200	1	16	5
1,200-1,300	1	13	8
1,300-1,400	1	12	8
1,400-1,500	1	10	10
1,500-1,600	1	10	10
1,600-1,700	1	7	14
1,700-1,800	1	7	14
1,800-1,900	1	6	16
1,900-2,000	1	6	16
2,000-2,500	1	6	16
2,500-3,000	0	4	0

4. *Three Basals*

Geographical Distribution.—Antarctic regions, and northward to northwestern Africa, the Caroline Islands, and British Columbia, except in the antarctic always in very deep water.

Systematic Distribution.—

Plicatocrinidæ

*Ptilocrinus**Gephyrocrinus**Hyocrinus**Thalassocrinus*

The frequency of each of these four types of asymmetry at different depths and temperatures is given in the tables on page 541 and in Fig. 4.

Depth (Fathoms)	Number of Genera with Asymmetrical Rays	Number of Genera with Symmetrical Rays	The Number of Genera with Asymmetrical Rays Expressed as a Percentage of the Number with Sym- metrical Rays
0-50	7	59	12
50-100	6	62	9
100-150	4	60	6
150-200	2	52	4
200-250	0	44	0
250-300	0	39	0
300-350	0	33	0
350-400	1	35	3
400-450	1	33	3
450-500	1	31	3
500-550	1	30	3
550-600	2	30	6
600-650	1	30	3
650-700	1	27	4
700-750	1	27	4
750-800	1	23	4
800-850	0	23	0
850-900	0	22	0
900-950	1	23	4
950-1,000	0	21	0
1,000-1,100	0	21	0
1,100-1,200	0	17	0
1,200-1,300	0	14	0
1,300-1,400	0	13	0
1,400-1,500	0	11	0
1,500-1,600	0	11	0
1,600-1,700	0	8	0
1,700-1,800	0	8	0
1,800-1,900	0	7	0
1,900-2,000	0	7	0
2,000-2,500	0	7	0
2,500-3,000	0	4	0

In the table showing the frequency at different depths the numbers in parentheses represent the actual cases, the other numbers being the percentage of the total number of genera in which the feature under consideration is found. This last is given in parentheses at the head of each column.

For a graphic representation of the data in the table on the lower part of page 541 see Fig. 5.

These frequencies group themselves as follows:

80°-60°	6.2
60-45	4.7
45-30	6.3
Below 30	2.0

or, segregating those occurring at the optimum temperature:

80°-65°	6.0
65-50	5.6
50-30	5.7
Below 30	2.0

Depth (Fathoms)	Number of Genera with More Than Five Rays	Number of Genera with Always Five Rays	The Number of Genera with More Than Five Rays Expressed as a Percentage of the Num- ber with Five Rays
0-50	1	65	1
50-100	2	66	3
100-150	2	62	3
150-200	2	52	4
200-250	2	42	5
250-300	1	38	3
300-350	1	32	3
350-400	2	34	6
400-450	2	32	6
450-500	2	30	6
500-550	2	29	7
550-600	2	30	6
600-650	2	29	7
650-700	3	25	12
700-750	3	25	12
750-800	3	21	14
800-850	3	20	15
850-900	3	19	16
900-950	3	21	14
950-1,000	3	18	16
1,000-1,100	3	18	16
1,100-1,200	3	14	21
1,200-1,300	3	11	27
1,300-1,400	2	11	18
1,400-1,500	2	9	22
1,500-1,600	2	9	22
1,600-1,700	2	6	33
1,700-1,800	2	6	33
1,800-1,900	1	6	16
1,900-2,000	1	6	16
2,000-2,500	1	6	16
2,500-3,000	0	4	0

The relation at different depths between the crinoids in which the disk is not radially symmetrical and those in which it is radially symmetrical is shown in the table on page 542 and in Fig. 6.

The relation at different depths between the crinoids in which one or more rays are dwarfed, or, more rarely, enlarged, and those in which all of the rays are of the same size is shown in the table on page 543 and in Fig. 6.

Depth (Fathoms)	Genera with Three Basals	Genera with Five Basals	The Number of Genera with Three Basals Expressed as a Percentage of the Number with Five Basals
0-50	0	66	0
50-100	0	68	0
100-150	0	64	0
150-200	0	54	0
200-250	0	44	0
250-300	1	38	2
300-350	1	32	3
350-400	1	35	3
400-450	1	33	3
450-500	1	31	3
500-550	1	30	3
550-600	1	31	3
600-650	1	30	3
650-700	1	27	4
700-750	1	27	4
750-800	1	23	4
800-850	1	22	4
850-900	1	21	5
900-950	1	23	4
950-1,000	2	19	10
1,000-1,100	2	19	10
1,100-1,200	2	15	13
1,200-1,300	2	12	16
1,300-1,400	2	11	18
1,400-1,500	2	9	22
1,500-1,600	2	9	22
1,600-1,700	3	5	60
1,700-1,800	3	5	60
1,800-1,900	3	4	75
1,900-2,000	3	4	75
2,000-2,500	3	4	75
2,500-3,000	1	3	33

The relation at different depths between the crinoids with more (less frequently less) than five rays, and those with five rays, is shown in the table on page 544 and in Fig. 6.

The relation at different depths between the crinoids with three basals and those with five is given in the table given above and in Fig. 6.

SUMMARY

Among the recent crinoids any wide departure from the normal close approximation to true pentamerous symmetry indicates unfavorable conditions of one or other of two main types, which are not mutually exclusive.

These two types are

1. INTERNAL UNFAVORABLE CONDITIONS, induced by incipient phylogenetical degeneration through type-senescence, as in the Plicatocrinidæ, which in the recent seas represent the almost exclusively palæozoic Inadunata; and

2. EXTERNAL UNFAVORABLE CONDITIONS, taking the form of

(a) *Phylogenetically excessive cold*, which, to cite one example, appears to be the determining factor in the asymmetry of the genus *Promachocrinus*; or of

(b) *Phylogenetically excessive warmth*, which appears to be the determining factor in the asymmetry of the family Comasteridæ.

INHERITANCE OF HABIT IN THE COMMON BEAN

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HABIT is the external form of a plant taken as a whole. It is usually described by a few general adjectives, such as erect, open, spreading, etc. However, to study the inheritance of plant habit, a detailed analysis of the real characters underlying habit must be made. It is usually found that the general outer appearance of a plant, its habit, is the result of a combination of independent characters, units, the recombination of which by crossing often results in plants much altered in appearance from the parent varieties. Characters usually unimportant may be found of primary importance in the formation of plant habit.

An example of such inheritance of habit is found in one of Webber's pepper hybrids (6). A cross was made between Red Chili, a variety with many erect fine branches, and Golden Dawn, with few, horizontal, coarse branches, both being of medium size. In the second generation recombination and segregation of the three character pairs occurred, although not in strict Mendelian proportions. The important feature of the results, however, lies in the apparent creation of a giant and a dwarf type, not by the appearance of new units by mutation, but simply by the transference of the characters fine and coarse branches. Hybrids having erect, many and coarse branches were giants, while those having few, horizontal and coarse branches were dwarfs. Other combinations of these characters gave intermediate forms.

The study here reported was made largely on third and fourth generation plants and a few second generation plants of hybrids made primarily for the study of pig-

mentation. The material worked with, owing chiefly to lack of knowledge of earlier generations, offered many limitations and is unsuited to a detailed analysis of the characters in question. As the plants were usually not more than six inches apart in the rows, the crowding in the later stages of development hindered accurate judgment of the habit type.

With reference to general habit bean plants are either pole or bush. Pole beans are commonly long twining vines, climbing when provided with poles or other support. The true bush type is usually short, erect and non-twining. There are also certain races of beans really intermediate between the true bush and pole types, the runner beans, which are non-climbing. Types classed as bush beans also occur, which are spreading and possess outstretched branches of a more or less runner-like character.

The following table contains a description of habit of varieties of beans considered in this discussion. The descriptions are from "American Varieties of Garden Beans" (5). The varieties observed agree with these descriptions except in the case of Mohawk, which is described as without runners. The strain of Mohawk isolated here produces runners.

TABLE I

DESCRIPTION OF BEAN VARIETIES

Pole Beans ALT¹

Golden Carmine—Small, good climber.

Creasback—Small, at first bush-like, poor climber when young.

Runner Beans ALt

White Marrow—Very large, very spreading, many runners.

Bush Beans ALT

Burpee Stringless—Large, medium, very erect when young, with a few shoots high above the plant, but more or less spreading when mature; no runners.

Giant Stringless—Same as above.

¹ For the meaning of these letters see page 550.

Semi-runner Forms Alt

Refugee—Very large, very spreading, many semi-runners.

Refugee Wax—Large, medium, very spreading, many runner-like branches.

Spreading Forms aLT or aLt

Longfellow—Large to medium, somewhat spreading, many outstretched branches, no real runners.

Kenny Rustless—Large, very spreading, almost runner-like branches.

Prolific Black Wax—Medium, more or less spreading, sometimes long outstretched branches, no real runners.

Erect Forms alT or alt

Black Valentine—Large, medium, fairly erect, occasional drooping branches, no real runners.

Blue Pod—Medium, erect, no runners or spreading branches.

Bountiful—Large, medium, fairly erect when young, but drooping when mature, no runners or decided spreading branches.

Burpee Kidney—Large, no runners, but usually drooping with fruit-laden branches and spreading when mature.

Burpee White Wax—Large, sometimes with drooping branches, but no real runners.

Challenge Black Wax—Very small, erect, no runners or spreading branches.

Curries—Medium, erect, no runners or spreading branches.

Davis Wax—Large, medium, erect, no runners.

Early Refugee—Medium, very erect, no runners or spreading branches.

German Black Wax—Medium, erect when young, usually borne down with fruit laden branches when mature, no runners.

Long Yellow Six Weeks—Medium, very erect, no runners or spreading branches.

Low Champion—Very large, usually erect, no runners or spreading branches.

Mohawk—Large, very erect, no runners, sometimes drooping when old.

Red Valentine—Medium, erect, no runners or spreading branches.

Round Yellow Six Weeks—Small, medium, very erect, no runners or spreading branches.

Wardwell—Large, medium, fairly erect, no runners.

Warren—Very large, usually erect, no runners or decided spreading branches.

Warwick—Medium, erect, no runners or spreading branches.

R. A. Emerson in his experiments on heredity of plant habit in beans found three main character pairs concerned, namely, length of plant axis, developed in various degrees; twining habit or circumnutation developed in various degrees or not at all; and lastly, the position of pods, axial or terminal. His data involve chiefly the latter character pair, which is inherited in a 3:1 propor-

tion, the axial position of pods being dominant. The position of pods or flowers influences plant habit in this manner: when flowers are formed at the growing tip of a main stem or branch, such a stem or branch must necessarily cease to elongate; on the other hand, if no flowers or fruits are formed at that point it may continue to grow indefinitely.

The habit of all the varieties of beans can be accounted for easily with only these three character pairs. In Table I the varieties here concerned have been grouped according to the probable presence or absence in them of the characters mentioned.

I have designated the axial position of the pods as A, the terminal position by a; long plant axis by L, short by l; a long axis was shown to be dominant over short in some of Mendel's crosses of beans (1). I have designated circumnutation by T and its absence by t, as, judging from Emerson's statements, and according to my own observations twining habit is dominant. The possible combinations of these characters are as follows:

HABIT TYPES

Type a, ALT....	Pole beans.
Type b, ALt....	Runner beans.
Type c, AlT....	Shoots.
Type d, Alt....	Semi-runners.
Type e, 1 aLT } 2 aLt }Spreading with long outstretched branches.
Type f, 1 aLT } 2 alt }Erect bush beans.

Type *a* comprises the pole beans, as the vines are of great length, both on account of long axis and not being checked by any terminal inflorescence, and as they can climb by virtue of circumnutation.

Type *b* comprises the runner beans. They are like the pole beans except that the climbing habit is not developed to any great extent, if at all. Between these two types it is difficult to draw sharp distinction, but the true runner probably lacks the factor for twining.

Type *c* probably represents the varieties which early send up a few shoots high in the air like Burpee Stringless. In such beans the growth of the main stems or branches is not entirely prevented by the absence of the character which produces a long axis, and as the climbing habit is more or less developed, the characteristic shoots are sent up.

Type *d* represents the semi-runners, caused by the short axis.

Combinations of type *c* and *e*₂ are the spreading varieties, with long outstretched branches. They are to be distinguished from runners by terminal inflorescences. Kenny Rustless is a representative of the *c* type of habit and probably Prolific Black Wax also.

The last two combinations, *f* and *f*₂, are the typical erect bush form, such as Blue Pod Butter and Challenge Black Wax.

Table II gives the possible crosses of these types and the *F*₂ proportions to be expected when the forms crossed are the most nearly typical. In the cases of typical forms, the *F*₂ types should be differentiated without much difficulty. A circumstance that must be looked upon as a possible cause of exceptions is the presence of unknown factors that cause variations in the intensity of the development of the twining habit and of the intermediate lengths between long and short axis. If there are various factors for length, as Emerson assumes to be the case in all quantitative characters (3), and if the twining habit is to be explained in much the same way, results may be considerably at variance with the expectations indicated in Table II. It must be remembered that the constitutions given for the varieties are only assumed.

At present, owing to circumstances mentioned before,

TABLE II

No.	Constitution	Type	<i>F</i> ₂ Proportions	
			<i>a</i> × <i>a</i>	<i>a</i>
1	ALT × ALT	<i>a</i> × <i>a</i>		<i>a</i>
2	ALT × ALt	<i>a</i> × <i>b</i>	3 <i>a</i> : 1 <i>b</i>	
3	ALT × AlT	<i>a</i> × <i>c</i>	3 <i>a</i> : 1 <i>c</i>	
4	ALT × Alt	<i>a</i> × <i>d</i>		

	ALT			7a	
	ALt	gametes		2	3b
	AlT				3c
	Alt				1d
				<hr/> 9a: 3b: 3c: 1d	
5	ALT × aLT	a × e		3a:	1c
6	ALT × aLt	a × e		7a	
	ALT	gametes		2	3b
	ALt				3e ₁
	aLT				1e ₂
	aLt				
				<hr/> 9a: 3b: 4e	
7	ALT × alT	a × f		7a	
	ALT	gametes		2	3b
	AlT				3e
	aLT				1f
	alT				
				<hr/> 9a: 3b: 3e: 1f	
8	ALT × alt	a × f	15a		
	ALT		6	7b	
	ALt		4		7c
	AlT		2	2	2 3d
	Alt				7e
	aLT				5
	aLt				3f
	alT				1
	alt		<hr/> 27a: 9b: 9c: 3d: 12e: 4f		
9	ALt × ALt	b × b		b	
10	ALt × AlT	b × c		9a: 3b: 3c: 1d	as in type No. 4.
11	ALt × Alt	b × d		3b: 1d	
12	ALt × aLt	b × e		3b: 1e	
13	ALt × aLT	b × e	7a		
	ALT	gametes	2	3b	
	ALt				3e
	aLT				1
	aLt				
			9	3	4
14	ALt × alT	b × f	27a: 9b: 9c: 3d: 12e: 4f	as in type No. 8.	
15	ALt × alt	b × f	7b		
	ALT	gametes	2	3d	
	AlT				3e
	aLT				1f
	alt				
			<hr/> 9b: 3d: 3e: 1f		

16	Alt × Alt	$e \times e$	e
17	Alt × Alt	$e \times d$	3e: 1d
18	Alt × aLT	$e \times e$	9a: 3c: 3e: 1f as in type No. 7.
19	Alt × alt	$e \times f$	
20	Alt × aLt	$e \times e$	3c: 1f
21	Alt × alt	$e \times f$	27a: 9b: 9c: 1d: 12e: 4f as in type No. 8.
	Alt		7c
	Alt		2 3d
	alt		3f
	alt		1
			9c: 3d: 4f
22	Alt × Alt	$d \times d$	d
23	Alt × aLT	$d \times e$	27a: 9b: 9c: 3d: 12e: 4f as in type No. 8.
24	Alt × aLt	$d \times e$	
	Alt		7b
	Alt		2 3d
	aLt	gametes	3e
	alt		1f
			9b: 3d: 3e: 1f
25	Alt × alt	$d \times f$	7c
	Alt		2 3d
	Alt		3f
	alt	gametes	1
	alt		9c: 3d: 4f
26	Alt × alt	$d \times f$	3d: 1f
27	aLT × aLT	$e \times e$	e
28	aLT × aLt	$e \times e$	e
29	aLT × alt	$e \times f$	3e × 1f
30	aLT × alt	$e \times f$	
	aLT		7e
	aLt		5
	alt	gametes	3f
	alt		1f
			12e: 4f
			3 : 1
31	aLt × aLt	$e \times e$	e
32	aLt × alt	$e \times f$	3e: 1f as in type 30.
33	aLt × alt	$e \times f$	3e: 1f
34	alt × alt	$f \times f$	f
35	alt × alt	$f \times f$	f
36	alt × alt	$f \times f$	f

only general notes on the behavior of various types of crosses can be given.

TYPE 2. ALT \times ALt

In the third generation of a cross of Creasback, a typical pole bean with White Marrow, a runner bean with probably a weak character for circumnutation, all lots were of axillary inflorescence. The habit of climbing was developed in various degrees so that classifications of types was difficult.

CROSS TYPE 6 OR 7. ALT + aLT or aLT

Notes on an early cross of Creasback by Prolific Black Wax indicate that the generation F_1 were pole beans, the generation F_2 segregating into 33 pole and 8 bush. The latter is probably a 3:1 proportion as expected. Whether all plants described as bush were of the spreading type does not appear from our records.

CROSS TYPE 8. ALT \times alt or aLT

In a cross of Creasback with Blue Pod, a typical bush bean, there occurs one strain of homozygous pole plants, and also in the F_4 generation heterozygous types. Pole and runner forms and bush forms of various types occur in the proportions of 9:7 in one lot and in another of 3:1, as might be expected in an F_4 generation. In another small lot occur plants with long outstretched branches, in another two plants of *c* type of habit. Evidently Blue Pod has the constitution alt.

The data from a cross of Creasback with Blue Pod do not signify much, as the types isolated happen to be constant, one a pole type and bush types, of which several are described as somewhat spreading. In one there occurs a runner bean.

Creasback and Warwick crosses in the F_4 generation behave consistently with the cross type, as assumed. In one lot, 12 have axial inflorescence and three terminal. Lots with spreading plants occur and one plant was noted which possessed a very long axis, along with a twining habit, but also terminal inflorescence. According to the

explanation of habit characters assumed, such a plant would have the formula aLt . Without a support which happened to have been placed near it, the peculiarity of the plant would not have been so noticeable.

A cross of Mohawk and Golden Carmine, a pole bean, gave in the F_2 generation 7 plants of the bush type and 28 plants more or less pole like. In the notes no separation of pole and runner beans were made, probably due to a lack of clear distinction between the two as occurs in many crosses.

CROSS TYPE 10. $ALt \times AIT$

White Marrow by Burpee Stringless is presumably a cross of this type. In one case the F_1 is described as a pole and in another as a runner bean. The F_2 generation results in 38 bush to 108 described as runner beans. This is consistent with expected results when the plant is described as a whole. The expectations are 12 pole and more or less pole like beans and four more or less bush like forms.

CROSS TYPE 12 OR 13. $ALt + aLT$ OR aLt

A cross of White Marrow, a runner variety, with Prolific Black Wax, which belongs to the type with spreading outstretched branches, gave 20 bush plants and 58 plants of the runner and pole types, no differentiation being made between the two. This is consistent with the assumed constitutions.

CROSS TYPE 14 OR 15. $ALt \times alt$ OR alt

White Marrow with Currie behaves according to expectation, giving in the F_2 generation 41 bush plants e or f in type, and 52 of the runner or semi-runner type.

In the cross of Blue Pod by White Marrow and its reciprocal, neither variety being pole in type, climbing plants apparently occur as well representative of most if not all of the other habit types. Some lots isolated were very erect, others spreading in various degrees; one lot is de-

scribed as having long tendril-like shoots above the plant, another along side of this had shorter shoots, perhaps ALT. Among the lots, all degrees of climbing were developed; one plant encountered was evidently aLT like the one mentioned in a previously discussed cross; plants with more or less outstretched branches were noted. Type notes on F_1 and F_2 generations of an earlier cross in type; F_2 segregates into 25 bush forms and 62 runners, are significant. The F_1 generation is described as pole probably including pole beans of the F_1 type. The ratio is disturbed by the lack of a clear understanding of the true basis for classification of plant type in beans. The F_2 of another cross involving the same varieties is noted as having 41 bush and 5 runner beans.

White Marrow and Burpee Kidney yielded two lots of bush beans and two heterozygote lots giving 6 plants with terminal inflorescence and 15 with axillary.

Red Valentine and White Marrow crosses give similar results. In an early cross, the F_2 generation plants have been grouped according to the general plant type, no attempt being made to separate intergrading types. The notes give the results of segregations as 75 bush and 136 runner beans. Later generation heterozygotes approach a proportion of 9 runner to 7 bush beans. The apparent behavior probably depends on whether the intermediate types are classed as runner or bush. In the cross in which only the F_4 generation was observed, only constant bush types seem to have been isolated.

CROSS TYPE 19 OR 21. ALT \times alt or aLT

Blue Pod crossed with Burpee is a representative cross of this type. Only in a few cases was the Burpee type, plants with shoots high in the air, observed, as most lots isolated were homozygous and erect. In the F_2 generation of an early cross, plants described as runners appeared. The proportion was 3 runners to 1 bush. Heterozygote lots descended from these plants segregated in the same manner, totaled 18 bush and 71 so-called run-

ners. The runners are probably really *c* in type or *c* and *d*.

In the cross of Giant Stringless and Blue Pod the parent types were both isolated. No semi-runners were noted, as would be the case if the cross were No. 21 in type.

CROSS TYPE 25 OR 26. Alt \times aLT or alt

Refugee Wax is a semi-runner bean. The F_3 isolated lots of this variety crossed with Blue Pod were all more or less erect. Some lots homozygous for axial branching were isolated, many individuals of which showed signs of climbing. The semi-running and climbing branches were short, confirming the assumption that neither variety used possesses the factor for a long axis. The climbing tendency exhibited shows that there must be strains of Blue Pod that possess T. Previous data are in harmony with this.

CROSS TYPE 29, 30, 34 OR 35. aLT or aLt \times alt or aLT

Many crosses of bush beans with those of spreading type give a 3:1 proportion in the F_2 and later heterozygous lots.

In Keeny Rustless, a variety of the spreading type, with its almost runner-like branches, by Red Valentine some lots with the spreading habit have been isolated, also more or less runner-like forms and one with the erect habit of Red Valentine. The axial and terminal inflorescence is inherited in a 3:1 proportion. Notes on type in one heterozygous lot show five erect and 10 plants with outstretched branches.

In the cross of Black Valentine and Prolific Black Wax one lot with outstretched branches was isolated; all others were of the erect type.

In the cross of Blue Pod Butter and Prolific Black Wax no spreading types with outstretched branches were noted, but this is not surprising, as in an F_4 generation the parent plants selfed for planting may not have hap-

pened to be of the spreading type, thus giving homozygous erect offspring.

In the cross of Golden Eyed Wax with Prolific Black, outstretched branches due only to axial inflorescence were noted.

Spreading plants of this nature also occur in the cross of Bountiful and Prolific Black Wax. In the latter two crosses the twining habit was more or less developed in the longer branches.

CROSS TYPE 34, 35, OR 36. $alT \times alT$, $alT \times alT$, OR
 $alt \times alt$

In the crosses of this type only erect bush beans without runners or spreading branches, should occur, although contorted stems might possibly appear. Such is the behavior of the following crosses of this type:

Low Champion \times Blue Pod Butter

Blue Pod Butter \times Golden Eyed Wax and reciprocal

Blue Pod Butter \times Mohawk and reciprocal

Challenge Black Wax \times Warwick

Currie \times Mohawk and reciprocal

Currie \times Red Valentine

Blue Pod Butter \times Warren

Bountiful \times German Black Wax

In the crosses, Challenge Black Wax by Davis Wax and Blue Pod Butter by Davis Wax, lots have been isolated with short shoots above the plants somewhat resembling the habit of Burpee Stringless and Giant Stringless. This behavior is unexpected if such a plant type is to be described by the formula ALT . The Davis Wax type used in the crosses may, however, have been of a different strain from that described in the table. This variety is the only one used in the crosses that was not under the observation of the writer, as its growth was discontinued the year in which these notes were taken.

While the factors discussed above primarily determine the plant habit, there are several others of secondary consideration. No special notes were taken with regard to

these. Some of them are mentioned in the following paragraph.

The character of the habit type is somewhat influenced by the amount of branching the plants exhibit; open, loose, bush beans are the result of few branches; the close, dense habit of some forms is caused by profuse branching. The size of a plant to some extent influences the habit, although not as much in small ones like Challenge Black Wax. In Warren the size of the plant probably causes it to droop. In some varieties the number and weight of the pods, as well as their position, cause some plants to droop and assume a spreading habit when old. Perhaps fineness and coarseness of branching affect habit.

One further matter that comes up for consideration is the question of the effect of environment upon plant habit. Its greatest effect, as would be supposed, seems to be upon such quantitative characters as length of the plant axis and probably the twining character to some extent. Instances of adverse conditions resulting in the almost total suppression of a character were noted in plants grown on poor soil. They exhibited the slender tips, typical of vines with axial inflorescence, but were otherwise bush-like and erect. The accelerating effects of very fertile soil on the growth of runner was also noted. However, the environmental explanation for the sudden appearance of runners among bush beans or of pole beans among typical runners is open to question. The most probable cause of such phenomena lies primarily in the regrouping of the unit characters of habit, combined at times with checking and accelerating factors external to the plant.

The investigations here reported offer a foundation upon which more extensive study on the subject might be based.

The following table suggests a few important cross types and the varieties which might be used to advantage:

CROSSES FOR FURTHER STUDY

No.	Type Number	Varieties	Plant Type
1	2	Golden Carmine \times White Marrow and reciprocal	$a \times b$
2	3	Golden Carmine \times Burpee Stringless and reciprocal	$a \times c$
3	4	Golden Carmine \times Refugee and reciprocal	$a \times d$
4	5 or 6	Golden Carmine \times Keeney and reciprocal	$a \times e$
5	7 or 8	Golden Carmine \times Challenge Black and reciprocal	$a \times f$
6	10	White Marrow \times Burpee Stringless and reciprocal	$b \times c$
7	11	White Marrow \times Refugee and reciprocal	$b \times d$
8	12 or 13	White Marrow \times Keeney and reciprocal	$b \times e$
9	14 or 15	White Marrow \times Challenge Black and reciprocal	$b \times f$
10	17	Burpee Stringless \times Refugee and reciprocal	$c \times d$
11	18 or 19	Burpee Stringless \times Keeney and reciprocal	$c \times e$
12	20 or 21	Burpee Stringless \times Challenge Black and reciprocal	$c \times f$
13	23 or 24	Refugee \times Keeney and reciprocal	$d \times e$
14	25 or 26	Refugee \times Challenge Black and reciprocal	$d \times f$
15	29 or 30	Keeney \times Challenge Black and reciprocal	$e \times f$

The Burpee crosses should be particularly watched to determine if the assumed set of factors A/T is the cause of the shoots and later spreading habit of the plant.

The axis should be studied by means of accurate measurement as far as possible. The judgment concerning circummutation would probably be necessarily more or less indefinite.

In crosses 4, 5, 8, 9, 11, etc. the type number should be determined.

The conclusions that can be drawn from observations reported in the preceding pages are:

1. That plant habit in beans is largely determined by the presence or absence of three characters which have been designated by the letters A, L, and T.

1. A, the presence of axial inflorescence permitting an indefinite growth, of the main stem and main branches, and a terminal inflorescence causing definite growth.

2. The length of the axis L, an important factor controlling plant habit and probably governed by a series of two or more factors for a length L_1 , L_2 , etc., which behave after the fashion of Emerson's hypothesis for the inheritance of quantitative characters.

3. The climbing habit is due to a factor for circum-

mutation. This factor may be called T. The cause of the various degrees of the climbing habit has not been determined with any degree of certainty. The contorted stems of erect bush forms are probably caused by T.

II. The factors A, L and T may be present in any possible combination, giving rise to the various habit types of beans.

III. When the types are crossed among themselves they behave approximately after the manner sketched in Table II.

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ON THE MODIFICATION OF CHARACTERS BY CROSSING¹

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IN the early years of Mendelian discovery there was much discussion concerning gametic purity in hybrids, and the question whether unit characters are modified on crossing was keenly debated. Convinced by the numerous instances in which Mendelian characters appear to be unmodified by crossing, many writers came to the conclusion that characters universally segregate without being modified or "contaminated" by association with other characters in the hybrid. That such a conclusion is far too sweeping is, however, indicated by many later results, and there is now a disposition to admit that changes in a character or the breaking up of a character may be effected through crossing. But some writers continue to look upon a unit character as an entity, which is unmodifiable and indestructible by hybridization.

Notwithstanding the admitted belief of Bateson and others that characters may be modified by crossing, I know of no extensive body of evidence that such modifications take place except the work of Castle and Phillips (1914) whose conclusions have not been fully accepted and are chiefly concerned with modification by selection. It therefore seemed worth while to direct attention to certain experimental results of a somewhat different kind which appear to show beyond cavil that modifications of characters sometimes result from crossing. The matter is an important one because it affects the old question of the swamping of new characters through crossing, as well as various other aspects of evolutionary theory.

¹ Read before the American Genetic Association, San Francisco meeting, August 3, 1915.

Anticipating the conclusions which will be reached in this paper, it may be pointed out that the swamping effect is not so serious a check upon progressive evolution as might be supposed, (1) because blending or modification of a new character only takes place in certain crosses and may be accompanied by segregation even in some of those, and (2) because Mendelian characters usually come out "pure" when crossed with the form from which they were derived. Hence when Mendelian characters arise through mutations in nature it may be expected that they will be able to perpetuate themselves and spread, especially when dominant, unless they place the organism at a disadvantage in the struggle for existence. The modification of a Mendelian character will come, not from crossing with its parent form but with a more distantly related species.

Some writers appear to believe that it is practically impossible to modify a unit character because it is represented in the germ plasm by a "gene" whose essential characteristic is its unmodifiability. But if we consider that each unit character is a *difference* which has arisen through a change in one element of the germ plasm, probably in a chromosome, then it would seem possible that if introduced into a foreign cytoplasm the chromosome may become subject to permanent modification.

Castle and Phillips (1914) have produced evidence from hooded rats tending to show that selection may modify a unit character in certain cases, although the nature of this result is not yet fully analyzed. They moreover show that the hooded character is modified by a cross. Davenport (1906) in his experiments with poultry, concluded that unit characters are frequently modified by crossing. He says (p. 80):

Very frequently, if not always, the character that has been once crossed has been affected by its opposite with which it was mated and whose place it has taken in the hybrid. It may be extracted therefrom to use in a new combination, but it will be found to be altered. This we

have seen to be true for almost every characteristic sufficiently studied—for the comb form, the nostril form, cerebral hernia, crest, muff, tail length, vulture hock, foot feathering, foot color, earlobe and both general and special plumage color. Everywhere unit characters are changed by hybridizing.

In crosses between *Enothera rubricalyx* and *E. grandiflora* I have studied with care the modifications which take place in the expression of the various character-differences in F_1 , F_2 and later generations. Many of the results have been recorded in detail elsewhere (Gates, 1914, 1915a, pp. 250–282). It need only be said that the foliage characters in F_2 form an absolutely continuous series so that it is impossible to apply to them usefully the unit-character conception. In F_3 a large number of races were obtained differing in many ways as regards their foliage, many of them breeding true and others varying within wide or narrow limits. Occasionally in back-crosses an apparently complete reversion takes place to one or other of the parents, but blending and fractionation of the characters is the rule.

It is, however, difficult to obtain critical evidence from the foliage because, while the original differences are sharply marked, yet it is always possible to assume that the continuous F_2 series and the numerous F_3 races result from the presence of many independent units.² I will therefore confine my attention to the sharp pigmentation character (R) of *rubricalyx*, for in the inheritance of this character crucial evidence may be obtained. The origin of this dominant unit-character through a single mutation, and the subsequent attainment of the duplicate condition (RR') for this character in some of the offspring of later generations (1915b), have been pointed out elsewhere. Here we will examine the modifications of R which take place when *rubricalyx* is crossed with *E. grandiflora*.

The main facts regarding the variability of R in these

² The inheritance of pubescence-differences shows similar features and can not be reasonably interpreted in terms of numerous units.

crosses have already been published (Gates, 1914, p. 244 and 1915a, p. 257) and need only be summarized here, to emphasize their significance. In the publications cited I had not yet recognized that the occurrence of 15:1 ratios in later generations of *rubricalyx* is significant as indicating that in such families the duplicate condition for R had been reached, even although other ratios such as 5:1 occur as well.

The F_2 generation of the crosses between *rubricalyx* and *grandiflora* contained 2,794 plants, in 20 of which the red bud-character R showed decided modification so as to be more or less intermediate between the two parents. Since each plant in bloom produces scores of buds simultaneously, and hundreds during the season, there is ample material for determining the exact degree of modification or development of the character in every individual. As will be seen from the original records, the 20 plants in which the color pattern was more or less modified were not all alike but formed a series, some being nearer the normal R than others. In most other F_2 plants sharp segregation took place, the buds being entirely either R or r without the slightest doubt in classification. In addition to the 20 plants above mentioned, there were, however, a certain number in which the character R was more or less underdeveloped, so that it was impossible to be certain whether they represented mere fluctuations or real modifications of the character.

The crucial test of modification is supplied by the F_3 generation. Two of these last-mentioned intermediate plants self-pollinated yielded offspring like themselves, without any tendency to segregate into the R and r types. These families numbered, respectively, 283 and 20 plants, so that in the former case at least any tendency to segregation could not fail to be observed. The buds of these plants were intermediate, the pigmentation was pale and was never fully developed on the hypanthium as is the case in *rubricalyx*. The whole population was then intermediate like the parent.

Another F_3 family (No. 149) was derived from an F_2 plant (65. III. 12) having sepals weak red with the color pattern as extensive as in *rubrinervis* 6 (*i. e.*, nearly the extreme condition), and in addition streaks of pale red on the hypanthium. This plant was therefore nearer *r* than *R*, and one may account for its occurrence through "contamination" before segregation took place in the germ cells of the previous generation. In pure *rubrinervis* or *grandiflora* I have never found even a trace of red on the hypanthium until the flower fades. The offspring of this plant numbered 186 individuals and their pigmentation fluctuated about that of the parent plant as a mean. This condition closely approximated that in *Æ. rubrinervoides* (1915c, p. 390), which may have originated in a similar way.

We must, therefore, conclude that plants which are intermediate in pigmentation breed true, at least in all cases tested, and that the degree of pigmentation in the parent is adhered to in the offspring whether the parent plant is an under-pigmented *R* or an over-pigmented *r*. In this aspect, the inheritance in such cases is quantitative and the offspring vary only within narrow limits.

The quantitative aspect is further emphasized when F_1 and F_2 hybrids of *Æ. grandiflora* and *Æ. rubricalyx* are crossed back with either parent. The pigmentation is much intensified when crossed back with *rubricalyx*, and greatly diluted when crossed with *grandiflora*. Thus in $(rubricalyx \times grandiflora) \times grandiflora$ if the female parent is heterozygous for *R*, segregation into *R* and *r* plants will occur in the offspring, but the *R* plants will be much paler than in the selfed offspring of the female parent.

Hence there are two somewhat antagonistic effects which have to be considered, (1) the segregation of *R* and *r* individuals, and (2) a permanent dilution of the pigmentation of the *R* individuals. The former effect can be explained by the meiotic mechanism which segregates

chromosome pairs. The latter effect may be due to a modification of the chromosomes themselves, or perhaps of the surrounding cytoplasm, or the inhibition in pigmentation may be explained by the presence of more numerous *grandiflora* chromosomes. Everywhere, in an accurate study of the inheritance of R, the quantitative as well as the qualitative (presence or absence) aspect has to be considered.

The dilution effect from crossing back with *grandiflora* has been tested in six families numbering 673 individuals and is always essentially the same. Although segregation into the R and r types takes place when the parent is heterozygous, yet R once diluted always remains so and apparently never gives rise to the original deeply pigmented condition. In other words, a permanently blended condition arises as regards the depth of pigmentation, although this will still segregate from the unpigmented condition in heterozygous plants.

It is not easy to furnish a complete explanation for this diluting effect. The permanent dilution of R through union with a *grandiflora* germ cell may perhaps be accounted for by the fact that in the heterozygote the chromosomes of *grandiflora* are closely associated in the same nucleus with those of the other parent. The chromosomes which are finally dissociated in the germ cells, after thousands or millions of mitotic divisions in association, might then be supposed to be somewhat modified. There are, however, difficulties with this view, since the absence-character, r, is usually not contaminated, but splits out sharply and almost invariably without any trace of red-production.

It is also difficult to account for the facts on the assumption that the cytoplasm has been permanently modified.

There is, however, one hypothesis which appears to meet the case. If all the *grandiflora* chromosomes are equally effective in inhibiting anthocyanin production in

the hybrids with *rubricalyx*—a not improbable hypothesis—then the dilution effect will be the same in F_1 or in crossing back, whenever an R chromosome is present in the next generation; and when such a chromosome is not present there will of course be complete absence from the buds of the *rubricalyx* pigment. On this hypothesis, in an original cross between *rubricalyx* and *grandiflora* a certain (observed) reduction in pigmentation occurs. When the F_1 hybrid is crossed back with *grandiflora* the additional *grandiflora* chromosomes thus introduced dilute or inhibit the color still further, while the presence or absence of the diluted R will depend upon whether or not the R chromosome from *rubricalyx* is present. It would thus appear to be unnecessary to assume that this chromosome is itself modified by its different nuclear and cytoplasmic environment.

In other words, the *grandiflora* chromosomes may be supposed to exert a mass effect in inhibiting the influence of the R chromosome. It is, of course, possible that in these circumstances the R chromosome itself may be permanently modified, but it seems possible to explain all the facts without making this assumption. In any case, whatever the *modus operandi*, there can be no question that the R character is permanently diluted by crossing with *grandiflora*, and the degree of dilution is increased every time the hybrid is again crossed back with that species.

Another noteworthy fact is that as the pigmentation becomes more dilute its morphological expression is more irregular. The color pattern of the bud begins to break up, and instead of continuous pigmentation of the whole bud a patchy effect will be produced. This spotted condition of the buds is very marked in certain families, *e. g.*, in the second generation of offspring from (*rubricalyx* \times *grandiflora*) \times *grandiflora* (see Gates, 1915a, Fig. 113, p. 280). When it appears it is found to persist in later generations. To account for this condition through the

accession of a "spotting factor" is a gratuitous assumption. Spotting appears rather to be the manner of expression of the character when the amount of pigment is small. It must be said, however, that in some families having no greater quantity of pigmentation there is a strong tendency for it to remain uniformly distributed, so that the whole bud is very pale red.

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SHORTER ARTICLES AND DISCUSSION

STUDIES ON INBREEDING. VI. SOME FURTHER CONSIDERATIONS REGARDING COUSIN AND RELATED KINDS OF MATING¹

IN the first of these studies² the writer dealt with the results, in so far as concerned coefficients of inbreeding, which would follow continued brother \times sister, parent \times offspring, and cousin \times cousin mating. Regarding matings of the latter type it is desired now to record certain further facts.

PEDIGREE TABLE I (HYPOTHETICAL)

TO ILLUSTRATE THE CONTINUED BREEDING OF FIRST-COUSIN \times FIRST-COUSIN
— SINGLE COUSINS

Δ	{ a b	{ c e	{ g h i j g h k l	{ m n o p m n o p m n u v	{ 1 2 3 4 1 2 3 4 1 2 9 10 1 2 3 4 1 2 5 6 1 2 3 4 1 2 7 8
Generation number	1	2	3	4	5

¹ Papers from the Biological Laboratory of the Maine Agricultural Experiment Station No. 85.

² AMER. NAT., Vol. XLVIII, 1913, pp. 577-614.

There are, of course, two possible sorts of first cousins, single and double. In the first case one of the parents of any individual is a brother (or sister) to the one of the parents of the other individual in the mating. In the second case, both the parents occupy this relation to the parents of the other individual in the mating.

These two sorts of first cousinship are shown in Pedigree Tables I and II.

PEDIGREE TABLE II (HYPOTHETICAL)

TO ILLUSTRATE THE CONTINUED BREEDING OF FIRST-COUSIN × FIRST-COUSIN
—DOUBLE COUSINS

Δ_4	$\left. \begin{array}{c} a \\ \\ \\ \\ \\ \\ b \end{array} \right\}$	$\left. \begin{array}{c} \left\{ \begin{array}{c} e \\ \\ \\ \\ \end{array} \right\} \\ \\ \\ \left\{ \begin{array}{c} e \\ \\ \\ \\ \end{array} \right\} \end{array} \right\}$	$\left\{ \begin{array}{c} g \\ \\ h \end{array} \right\}$ $\left\{ \begin{array}{c} i \\ \\ j \end{array} \right\}$ $\left\{ \begin{array}{c} g \\ \\ h \end{array} \right\}$ $\left\{ \begin{array}{c} i \\ \\ j \end{array} \right\}$	$\left\{ \begin{array}{c} k \\ \\ l \end{array} \right\}$ $\left\{ \begin{array}{c} m \\ \\ n \end{array} \right\}$ $\left\{ \begin{array}{c} k \\ \\ l \end{array} \right\}$ $\left\{ \begin{array}{c} m \\ \\ n \end{array} \right\}$ $\left\{ \begin{array}{c} k \\ \\ l \end{array} \right\}$ $\left\{ \begin{array}{c} m \\ \\ n \end{array} \right\}$	$\left\{ \begin{array}{c} o \\ p \\ q \\ r \\ o \\ p \\ q \\ r \\ o \\ p \\ q \\ r \\ o \\ p \\ q \\ r \\ o \\ p \\ q \\ r \\ o \\ p \\ q \\ r \end{array} \right\}$
Generation number	1	2	3	4	5

The values of the coefficients of inbreeding for continued single and double cousin mating are shown in Table I.

It will be seen that Pedigree Table I and the third column of Table I are different from the corresponding values given on pages 591 and 592 of the earlier paper. The present values should be substituted for the earlier ones, which were based upon

the erroneous assumption that half the double-cousin values would give single-cousin values.

TABLE I
VALUES OF THE SUCCESSIVE COEFFICIENTS OF INBREEDING IN THE CASE OF
CONTINUED COUSIN MATING

Coefficient of Inbreeding	Ancestral Generation Included	Coefficient for Single Cousins	Coefficient for Double Cousins
Z_0	1	0	0
Z_1	2	0	0
Z_2	3	25.00	50.00
Z_3	4	50.00	75.00
Z_4	5	68.75	87.50
Z_5	6	81.25	93.75
Z_6	7	89.06	96.98
Z_7	8	93.75	98.44
Z_8	9	96.48	99.22
Z_9	10	98.05	99.61
Z_{10}	11	98.93	99.80
Z_{11}	12	99.41	99.90
Z_{12}	13	99.68	99.95
Z_{13}	14	99.83	99.98
Z_{14}	15	99.91	99.99
Z_{15}	16	99.95	99.994

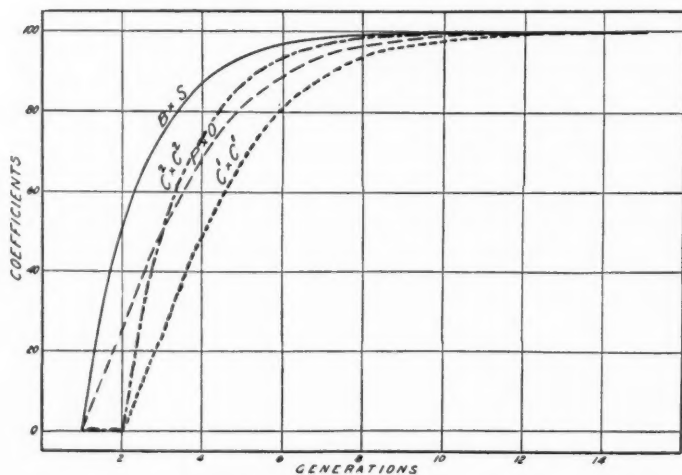


FIG. 1. Curves of inbreeding, showing (a) the limiting case of continued brother x sister breeding, wherein the successive coefficients of inbreeding have the maximum values; (b) continued parent x offspring mating; (c) continued first-cousin x first-cousin mating where the cousinship is double ($C^2 \times C^2$), and (d) continued first-cousin x first-cousin mating where the cousinship is single ($C^1 \times C^1$). The continued mating of uncle x niece gives the same curve as $C^1 \times C^1$.

The data of Table I are given graphically in Fig. 1, together with the curve for brother \times sister and parent \times offspring.

From the table and figure it is seen that with continued inbreeding according to any one of these four types the coefficient approaches the value 100. The rate of approach is different, however, in the different cases. The curves fall into two pairs. The brother \times sister and the double cousin curves are precisely alike so far as concerns their curvature or shape at any given point. Similarly, the parent \times offspring and single cousin curves are of the same shape. *The essential point of difference is that the cousin curves lag a generation behind the others.*

Let us now consider the question of the degree of inbreeding following continued matings of the avuncular type of relationship. Pedigree Table III gives a pedigree in which each mating is of uncle \times niece.

PEDIGREE TABLE III (HYPOTHETICAL)

TO ILLUSTRATE THE MATING OF UNCLE \times NIECE

				$\left\{ \begin{matrix} m \\ n \end{matrix} \right.$	$\left\{ \begin{matrix} u \\ v \\ w \\ y \\ m \\ n \\ z \\ l \\ m \\ n \\ o \\ p \\ q \\ h \\ 2 \\ 3 \\ m \\ n \\ o \\ p \\ q \\ h \\ r \\ g \\ h \\ i \\ k \\ d \\ s \\ t \end{matrix} \right.$
		$\left\{ \begin{matrix} c \\ d \end{matrix} \right.$	$\left\{ \begin{matrix} g \\ h \end{matrix} \right.$	$\left\{ \begin{matrix} o \\ p \end{matrix} \right.$	$\left\{ \begin{matrix} n \\ a \\ z \\ l \\ m \\ n \\ o \\ p \\ q \\ h \\ 2 \\ 3 \\ m \\ n \\ o \\ p \\ q \\ h \\ r \\ g \\ h \\ i \\ k \\ d \\ s \\ t \end{matrix} \right.$
	$\left\{ \begin{matrix} a \\ b \end{matrix} \right.$	$\left\{ \begin{matrix} e \\ f \end{matrix} \right.$	$\left\{ \begin{matrix} i \\ j \end{matrix} \right.$	$\left\{ \begin{matrix} g \\ h \end{matrix} \right.$	$\left\{ \begin{matrix} g \\ h \\ i \\ j \\ k \\ d \\ s \\ t \end{matrix} \right.$
X					
Generation number	1	2	3	4	5

From this table it appears that the values of the coefficients of inbreeding will be exactly the same for this type of mating as in the case of single cousin mating. Or, in other words, Z's form the following series.

TABLE II

VALUES OF COEFFICIENTS OF INBREEDING FOR CONTINUED
UNCLE \times NIECE MATING

Coefficient	Number of Ancestral Generations	Value of Coefficient
Z_0	1	0
Z_1	2	0
Z_2	3	25.00
Z_3	4	50.00
Z_4	5	68.75
Z_5	6	81.25
etc.	etc.	etc. as in Table I

From the data presented in this and former papers it is clear that inbreeding continued for about ten generations, quite regardless of the *type* of mating, provided only it be *continuously* followed, leads to within one or two per cent. of complete "concentration of blood." The bearing of this result upon the general question of the degree of inbreeding which exists in the ancestry of our domestic animals to-day is obvious. To consider but a single case: In 1789³ a law was passed prohibiting the importation of cattle into the Island of Jersey. Hence it follows that all pure-bred Jersey cattle of the present time must be of the descendants of the relatively few animals on the Island in 1790. Taking three years as about the average generation interval in cattle, this means about forty generations since the Island was closed to importation. The concentration of lines of descent which must have occurred in this time merely by the dropping of lines and quite regardless of the type of mating is obvious. This is not the place to go in detail into the discussion of inbreeding in Jerseys, especially as I hope shortly to publish the results of an extensive study of this matter, but it seems desirable to emphasize the bearing of such hypothetical pedigrees for particular types of mating as are given in this and earlier papers, on the general problem of inbreeding.

It is possible to extend now somewhat the table of general equations given by Jennings⁴ for coefficients of inbreeding after

³ *Teste* Rees's Encyclopedia and H. S. Redfield, *Natl. Stockman and Farmer*, December 15, 1892.

⁴ *AMER. NAT.*, Vol. XLIII, p. 695, 1914.

n generations of each particular type of mating. We have the following values, where n denotes the number of ancestral generations concerned, or, as Jennings puts it, the number of successive inbreedings which have taken place.

Type of Mating	Coefficient of Inbreeding
Self-fertilization	$\frac{2^n - 1}{2^n}$
Brother \times sister	$\frac{2^n - 2}{2^n}$
Cousin \times cousin, single	$\frac{2^n - 2n}{2^n}$
Cousin \times cousin, double	$\frac{2^n - 22}{2^n}$ { from $n = 2$ to $n = \infty$
Parent \times offspring	$\frac{2^n - n - 1}{2^n}$
Uncle \times niece	$\frac{2^n - 2n}{2^n}$

RAYMOND PEARL

AN ATTEMPT TO PRODUCE MUTATIONS THROUGH HYBRIDIZATION

THERE is no more interesting problem to the experimental evolutionist than the one relating to the cause or causes of the origin of mutations. Until we are able to solve this problem we can only accept what the gods give in our breeding experiments. When a mutation arises it is usually a simple process to produce a pure stock. By mutation is meant any deviation from the normal type which reappears in some of the descendants. In the following experiment most of the abnormalities that were found never reappeared in the offspring.

My experiments have been confined to the fruit fly, *Drosophila ampelophila*, a species kept for years "under cultivation" at Columbia University. This species has proved to be very plastic, throwing off great numbers of mutant forms. At the suggestion of Dr. T. H. Morgan I crossed some of these mutants with wild stock of the same species from widely separated localities in order to test whether through hybridization mutations arise in greater numbers than in inbred stock.

The idea that new forms arise from crossing more or less closely related species is an old one. One finds many references in Darwin's works to this conception. For instance, in the "Origin of Species" Darwin says:

When mongrels and the more fertile hybrids are propagated for several generations, an extreme amount of variability in the offspring in both cases is notorious; but some few instances of both hybrids and mongrels long retaining a uniform character could be given. The variability, however, in the successive generations of mongrels is, perhaps, greater than in hybrids.

One of the causes of ordinary variability . . . is . . . that the reproductive system from being eminently sensitive to changed conditions of life, fails under these circumstances to perform its proper function of producing offspring closely similar in all respects to the parent form.

From "Plants and Animals under Domestication" we find the following.

Crossing, like any other change in the conditions of life, seems to be an element, probably a potent one, in causing variability.

A variation to be effective in species formation must reappear in some of the descendants. That a variation could, through selection within a *pure strain* be increased or decreased in the direction of selection to form a stable species has been seriously questioned since Johannsen's classic experiments. It is well understood, on the other hand, how selection in a *mixed population* could cause the variation to move in the direction of selection up to a certain point.

The first mutant stock selected for the experiment was cherry club vermillion. The factors for these three characters are linked together and are also linked with sex; the second stock was black pink bent, which has the three factors independent of each other and none is linked with sex. These factors are supposed to lie in the second, third and fourth chromosomes, respectively. The third stock was black purple vestigial are speck, which has the five factors linked together. They lie in the second chromosome. A stock from France was crossed to the mutant stock several months after the other crosses were made, and eosin tan vermillion was substituted for the cherry club vermillion, and pink kidney sooty rough for the black purple vestigial are speck stock because flies of these particular stocks were not to be had at the time desired.

These forms were chosen because it was thought that if mutations do arise from hybrid forms there would be more probability of their origin from a mutant varying in several characters when crossed to wild than if it varied in only one character. Also by using stock containing several recessive characters a check could

be placed upon any variant from the expected classes due to contamination; for the variant, if arising from the cross, would give some offspring in the F_2 generation with some of the recessive characters. However, extreme care was taken to avoid contamination and at no time was there reason to suspect it in any of the cultures.

The wild stocks used were from Arkansas, California, Massachusetts, Illinois, Minnesota, Ohio, Wyoming, Porto Rico, Cuba, Australia and France. The totals of the F_2 generations are as follows:

	Ch. Cl. Ver.	Bl. Pk. B.	Bl. P. Vg. Arc. Sp.
Arkansas	1,162	307	198
California	859	715	332
Illinois	211		287
Massachusetts	1,078	681	1,013
Minnesota	771	274	
Ohio	506	1,612	370
Wyoming	925	150	
Porto Rico	151	207	
Cuba			819
Australia	469	401	548
France	814	951	826
Total	6,946	5,298	4,393

This gives a grand total of 16,637 flies. It should be noted that these flies were examined with the greatest care under a binocular microscope. Each fly was turned over separately and every part carefully examined.

From the cherry club vermilion crosses the following abnormal forms were found; three gynandromorphs; twenty-four flies with more or less beaded wings; two flies with three cross veins on the wings; one truncate; and two flies with abnormal abdomen.

The abnormal forms from the crosses with black purple vestigial are speck were, sixty-three with more or less beaded wings; one truncate; one abnormal abdomen; one fly with five legs; and four flies with a projection from the posterior cross vein toward the base of the wing.

From the black pink bent crosses were found two beaded; one abnormal abdomen; three truncate; and one called furrowed because of the furrows in the eyes due to the foreshortening of the head.

This gives a total of 109 abnormal forms or one abnormal in

every 152 flies. But 89 of these abnormalities were flies with beaded wings. This character is very variable; some of the flies had only a few bristles missing from the margin of the wings, while others had both the outer and inner margins of the wings serrated. The character has been recurring in the stock so frequently that it can scarcely be ascribed to outcrossing. Many of these flies were mated, but they either did not leave offspring, or the character did not reappear in the F_2 generation.

The three gynandromorphs are not to be considered as mutants. The data here show that gynandromorphs occur once in about five thousand five hundred times.

Flies with truncate wings are of occasional occurrence in the laboratory stock, as are also those with abnormal abdomen; hence, flies with these characters are not to be considered as due necessarily to the outcrossing. The truncate would not breed and the abnormal abdomen character did not reappear in the F_2 generation. If a character does not reappear in the F_2 generation it is considered to be of somatic and not of germinal origin, unless an environmental condition is necessary for the expression of the changed character.

The abnormality of the fly with five legs may have been the result of accident, for the character did not reappear in the F_2 generation.

Three characters were found to be inherited; the one called "furrowed," which arose from the cross of black pink bent with wild stock from Massachusetts; the one with a projection from the posterior cross vein toward the base of the wing, called "tau," which arose from the cross of black purple vestigial arc speck with wild stock from Illinois; but since this stock had just been received from Illinois, and since the character appeared in four of the flies, it is suspected that the character was recessive in the wild stock and not due solely to the cross. Also from cherry club vermilion crossed to stock from Arkansas arose two males with three cross veins on the wings and a disturbance of the ommatidia of the eye. This character is called "warty."

Pure stocks of flies with these characters have been bred for many generations and each continues to breed true. "Warty" has many other characters than the modification of the eyes, *e. g.*, beaded wing, spread wing, from two to five cross veins on the wings, abnormal abdomen and disarranged hairs on the thorax. The females are sterile and the race is maintained

by crossing the males to their heterozygous sisters. The character is not sex linked; it decreases the viability of the flies, but more than this can not be said at present. Work is being continued on this character and on flies with the character "tau."

"Furrowed" is characterized by having the head foreshortened, which causes indentations or furrows in the eyes; also the spines on the scutellum are stumpy. The last character is of importance in determining some of the flies, as a female will sometimes occur without any disturbance of the eyes.

This character arose in a male which was crossed to a wild female. The F_2 generation gave normal females and half the males were normal and half were furrowed. This established the fact that the character followed the distribution of the sex chromosome. The position of the gene in the chromosome was next determined according to the theory that the genes in any chromosome are arranged in a linear series.¹ Crosses were made with eosin miniature, sable forked, and with vermilion barred. Because of the low fertility of the furrowed females the cross was always made with the furrowed males. Consequently, the males alone are considered in the counts given below.

EOSIN MINIATURE ♀ BY FURROWED ♂

F ₂ males..	{	Normal	3	Furrowed	67
		Eosin miniature furrowed. 1		Eosin miniature	75
		Eosin long	3	Miniature	31
		Miniature furrowed	0	Eosin long furrowed	28

In the first column are the cross-over classes between miniature and furrowed and the per cent. of these to the whole number is 3.4. Then the gene which determines the character "furrowed" is supposed to lie 3.4 points beyond miniature, or at 39.6.

SABLE FORKED ♀ BY FURROWED ♂

F ₂ males..	{	Furrowed sable forked... 1	Sable forked	61	
		Normal	8	Furrowed	105
		Forked	3	Furrowed forked	15
		Furrowed sable	0	Sable	16

In the first column are the cross-over classes between furrowed and sable and these are 5.7 per cent. of the entire number. Then furrowed lies at a point 5.7 to the left of sable, or at 37.3.

¹ Sturtevant, *Jour. Ex. Zool.*, '13.

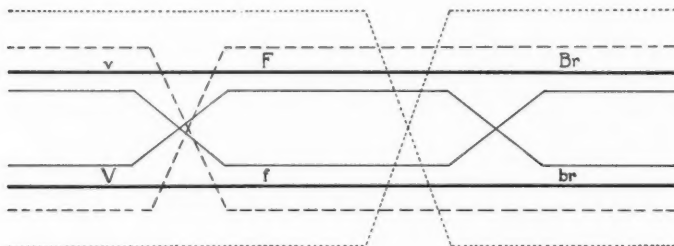
VERMILION BARRED ♀ BY FURROWED ♂

F ₂ males.	Bar	6	Vermilion bar.....	86
	Vermilion furrowed	3	Furrowed	102
	Normal	0	Furrowed bar.....	15
	Vermilion furrowed bar... 0		Vermilion	28

The cross-over classes between vermilion and furrowed are the bar and vermilion furrowed classes of which there are nine, which is 3.75 per cent. of the entire number. Vermilion is at 33, hence the gene for furrowed lies at 36.75.

The cross-over classes between furrowed and bar are the furrowed bar and the vermilion classes of which there are 43 which is 18 per cent. Then furrowed lies 18 points to the left of bar or at 39.

The discrepancy in these results is due to the low viability of the furrowed flies, yet the results agree fairly well, varying from 36.75 to 39, giving an average of 38.1, which is considered as the relative position of the gene for furrowed in the sex chromosome.



The accompanying diagram will aid in understanding the cross-over classes. The heavy straight lines represent the paired sex chromosomes which a heterozygous female has received from her parents. The upper one, which carries vermilion bar, was received from the female parent and the lower, carrying furrowed, was received from the male parent. Each of the sons of this heterozygous female receives one of these chromosomes which determines what it shall be with reference to these special characters. In about 75 per cent. of the cases the sons receive these chromosomes without any interchange of substance between the two as is shown by the two straight lines which represent the non-cross-over classes. When there is an interchange

of material between the two chromosomes as indicated by the crossed lines, then males arise with a different arrangement of the characters from that which had appeared in the grandparents.

In the diagram *v*, *f* and *Br* stand for vermilion eye, furrowed eye, and bar eye, respectively; while *V*, *F* and *br* stand for the normal allelomorphs of these characters, *i. e.*, red eye, not furrowed and not bar. Reading from the left the top dotted line includes *v*, *F* and *br*, but since *F* and *br* are normal the flies will differ from normal forms in the one character alone, *viz.*, vermilion. The dotted line below includes *V*, *f* and *Br*, hence the males receiving this chromosome are furrowed bar. Referring to the table showing the cross between a vermilion bar female with a furrowed male we see that there were 28 vermilion and 15 furrowed bar flies. Reading from the left again and omitting the normal allelomorphs, the upper dash line includes vermilion and furrowed and the lower dash line includes bar alone. The table shows that there were only three vermilion furrowed and six bar males, hence the interchange of material between vermilion and furrowed took place less frequently than it did between furrowed and bar. Since the per cent. of crossing over between any two genes is taken as the index of the relative distance between those genes, then furrowed lies much closer to vermilion than it does to bar.

The fine lines represent double crossing over, of which no representatives were found in this cross.

SUMMARY AND CONCLUSIONS

Crosses were made with mutant stocks of *Drosophila* with wild stock from many localities in the United States, from the West Indies, France and Australia in order to discover, if possible, if hybridization is an essential factor in the formation of mutant races. From 16,637 flies of the F_2 generation seven flies arose which varied from the normal type and which bred true. If we discard the four with the character "tau" for reasons given above, then the result is narrowed to three flies with two characters. This gives one mutant to every 5,545 flies. Therefore, a mutation has occurred so seldom that we can scarcely attribute hybridization as its cause. It is highly probable that if the same number of wild flies had been reared under

favorable conditions for the survival of any new forms that appeared just as many mutations would have been found as in the above experiment. In the light of these results we can attribute the origin of mutations only to chance, since hybridization as a causal agent does not occupy a privileged position relative to the effect.

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LINKAGE AND SEMI-STERILITY

THE Florida velvet bean (*Stizolobium deeringianum*) has normal pollen and embryo-sacs; it flowers (when sown in May) early in September; and has pigmented (mottled) seed-coats. The Yokohama bean (*Stizolobium hassjoo*) has also normal pollen and embryo-sacs; it flowers in July; and has its seed-coats unpigmented. The first-generation hybrids of Florida by Yokohama had half their pollen and embryo-sacs aborted (1, 2); flowered at the end of August; and had more or less pigmented seed-coats. In the second generation, half of the plants had normal pollen and embryo-sacs, and half showed semi-sterility (1, 2). These plants flowered from July to September, the majority being late. About three-quarters had pigmented seed-coats; and one-quarter, colorless seed-coats.

Most of the semi-sterile plants, and also most of the plants with pigmented seed-coats, were late in flowering. The semi-sterile plants, however, were not later than the fertile, in the second generation of the *Florida by China* cross. Hence there is no necessary connection between semi-sterility and lateness. A random sample of five second-generation plants of the Florida by Yokohama cross gave one family with pigmented seed-coats, one family with colorless seed-coats, and three families segregating into pigmented and colorless in about the ratio 3:1. Hence the pigmentation of the seed-coat is not a mere physiological consequence of lateness, but is determined by a definite factor. If *K* is the factor from the Florida concerned with semi-sterility; *P*, a factor concerned with pigmentation of seed-coat; and *H*, the main factor for lateness; then *K* and *H* are strongly coupled in the gametes of the first-generation plants, as are also *P* and *H*. *K* and *P* show secondary coupling.

The data follow.

SEMI-STERILITY AND LATENESS

Second generation of Florida by Yokohama

Seeds sown early in May

(Classes are approximately fortnights)

	1	2	3	4	5	6	Totals
Fertile plants	14	29	19	7	5	7	81
Semi-sterile plants	6	10	11	29	10	9	75

The average of the semi-sterile is about a fortnight later than that of the fertile. If we divide the plants into those flowering before and after August 11, we have:

	First Month	Second and Third Months
Fertile	43	38
Semi-sterile	16	59

A calculation, based on the hypothesis used for semi-sterility (1), shows that the crossing-over (3) between *K* and *H* is probably less than 17 per cent.

SECOND GENERATION OF FLORIDA BY YOKOHAMA

Seeds sown early in June

	2	3	4	5	6	Totals
Fertile	7	24	33	5	8	77
Semi-sterile	4	17	28	14	25	88

The fertile plants are earlier than the semi-sterile; though the average difference is less than in the early planting, because, as usual, the first-early plants are more affected by late planting than are the later plants.

PIGMENTATION OF SEED-COAT, AND LATENESS

Second Generation of Florida by Yokohama

Early sowing

	1	2	3	4	5	6	Totals
Unpigmented seed-coats ...	16	18	6	0	0	1	41
Pigmented seed-coats	4	22	25	35	14	12	112

Thus most plants with unpigmented seed-coats are early. A calculation again shows that the amount of crossing-over is probably under 23 per cent.

SECOND GENERATION OF FLORIDA BY YOKOHAMA

Late sowing

	2	3	4	5	6	Totals
Unpigmented seed-coats	8	20	12	1	2	43
Pigmented	3	21	46	17	31	118

This confirms the results from the early sowing.

PIGMENTATION OF SEED-COAT AND SEMI-STERILITY

The coupling between *K* and *P* is given from the following:

SECOND GENERATION OF FLORIDA BY YOKOHAMA

	Unpigmented	Pigmented	Totals
Fertile	45	110	155
Semi-sterile	39	120	159

The excess of pigmented semi-sterile and of unpigmented fertile testifies to a slight coupling, and calculation shows that there is probably about 35 per cent. of crossing-over.

According to the hypothesis (1), fertile second-generation plants should be mainly homozygous for *H* (or *h*) and *P* (or *p*); while semi-sterile plants should be mainly heterozygous for these factors. This is being further tested.

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